Chapter 6
Ecosystem Dynamics

6.1 Introduction

An ecosystem, as defined by Odum and Barrett (2005) is a functional unit that "includes all the organisms in a given area interacting with the physical environment so that flows of energy and materials leads to clearly defined biotic entities and cycling of materials between living and nonliving components". It is the first complete ecological unit from which we can metaphorically see the forest for the trees. From this perspective, the carbon balance of mangrove ecosystems and the cycling of nitrogen and mineral elements in relation to ecosystem development (that is, young versus old ecosystems) will be assessed, including how the delicate balance of these cycles are (or aren't) altered by human disturbance. Finally, some holistic models of mangrove food web dynamics will be examined before moving on to how an energetics perspective can help delimit the key conservation and management issues of sustainability and ecosystem services.

6.2 Material Exchange: The Outwelling Concept

Tides represent a form of energy subsidy for mangrove ecosystems, in that tides (and to a lesser extent, waves) do the work of transporting particulate and dissolved materials, gases, and other by-products between the forest and the adjacent coastal zone (see Chapter 3). This function is a corollary of source-sink energetics in which excess organic production by mangroves (the source) is exported to the less productive, coastal nearshore zone (the sink). In reality, of course, energy and materials are also imported into mangrove ecosystems by the same tides. The idea that the fertility of estuarine wetlands may contribute nutrients to sustain productivity in the adjacent nearshore came from a brief commentary by Eugene Odum (1968) in which he suggested that high productivity in coastal areas results either from 'upwelling' of deep water or from 'outwelling' of nutrient and organic detritus from fertile hot spots such as salt marshes, reefs, and macrophyte beds (Odum 2000). The 'outwelling' hypothesis generated a great deal of subsequent research

effort on the exchange of particulate and dissolved nutrients between wetlands and adjacent coastal waters, including a number of research programs on whether or not mangroves outwell substantial amounts of material to the tropical coastal zone.

After nearly 3 decades of research, we now know that the amount of organic detritus potentially available for export from mangroves is influenced by many factors, including net forest primary production, tidal range, ratio of mangrove to watershed area, lateral trapping, high salinity plugs, total mangrove area, frequency of storms, amount of rainfall, volume of water exchange, and the extent of activities of crabs and other litter-feeding fauna (Twilley 1988). The number of factors and their nature is such that each system is unique; some mangroves export nutrients and some do not.

6.2.1   Carbon Export to the Coastal Ocean and the Atmosphere

Most data on material exchange involve estimates of the export of particulate organic carbon, mainly as litter, from mangrove estuaries. Updating the carbon export data in Table 6.1 from Jennerjahn and Ittekkot (2002) gives a revised annual carbon export estimate of 15.3 mol C m^{-2} (Table 6.1). Assuming that the total mangrove area worldwide is 15,763,000 ha (FAO 2003), multiplying both numbers gives a mean value of 29 Tg $year^{-1}$. This estimate is at the low end of the range (30–50 Tg $year^{-1}$) first calculated by Twilley et al. (1992) and less than the 46 Tg $year^{-1}$ estimated by Jennerjahn and Ittekkot (2002). Further assuming a mean above-ground net primary productivity of 44.5 mol C m^{-2} $year^{-1}$ (Section 2.5.3), the export of POC equates to 32%, or roughly one-third, of total NPP. Obviously, the amount of export will vary greatly among estuaries depending on the relative importance of the factors listed above, but these estimates indicate that mangrove POC export

Table 6.1 Estimates of export of particulate organic carbon (mol C m^{-2} $year^{-1}$) from mangrove estuaries worldwide

Location	Export	Reference
Rookery Bay, Florida	5.3	Twilley (1985b)
South Florida	15.5	Twilley (1985b)
Tuff Crater, New Zealand	9.3	Woodroffe et al. (1985a, b)
Darwin Harbour, Australia	26.7	Woodroffe et al. (1988), Burford et al. (2008)
Matang, Malaysia	19.1	Gong and Ong (1990), Alongi et al. (2004a)
Klong Ngao, Thailand	0.1	Wattayakorn et al. (1990)
Itacuruca, Brazil	18.3	Lacerda (1992)
Fly River, Papua New Guinea	23.8	Robertson and Alongi (1995)
Missionary Bay, Australia	27.7	Alongi (1998)
Hinchinbrook Channel, Australia	10.4	Ayukai et al. (1998)
Sawi Bay, Thailand	5.9	Alongi et al. (2000c)
Caeté estuary, Brazil	16.1	Dittmar et al. (2001)

could account for 10–11% of the total input of terrestrial carbon into the ocean and 12–15% of the total carbon accumulation in sediments on the continental margin. Similarly, Dittmar et al. (2006) estimate that about 10% of terrestrially-derived DOC exported to the ocean is contributed by mangroves. Given their small area relative to other ecosystems, mangroves are thus contributing disproportionately to POC flux to the coastal ocean.

Naturally, the largest exports come from macrotidal and mesotidal estuaries (e.g., Darwin Harbour, Missionary Bay, and the Fly River), and some of the smallest exports come from microtidal systems (e.g., Sawi Bay), underscoring the importance of tidal regime and the fact that ebb tides tend to be stronger than flood tides. Other studies have measured net export, but either the amount of material was unquantified or difficult to determine from the information provided (Hemminga et al. 1994; Harrison et al. 1997; Rivera-Monroy et al. 1998; Ovalle et al. 1999; Davis et al. 2001; Pradeep Ram et al. 2003).

Clearly, most mangroves export POC, but the patterns of both POC and DOC exchange often differ within the same estuary with change in season. For example, in Missionary Bay in northern Australia, the Coral Creek mangroves annually export, on average, $27.7\,mol\ POC\ m^{-2}$; DOC exchange varies seasonally with net import during the summer and a slight import overall of $0.6\,mol\ DOC\ m^{-2}\ year^{-1}$ (Robertson et al. 1992).

In other systems, such as in basin forests or in microtidal systems, a greater proportion of material is exported in dissolved form (southwest Florida: Twilley 1985b, Sawi Bay, Thailand: Alongi et al. 2000c). In the only shelf-scale study of mangrove export of DOC, Dittmar et al. (2006) found greater outwelling of DOC ($12\,mol\ C\ m^{-2}\ year^{-1}$) than did earlier small-scale studies in the same region off Brazil ($4\,mol\ C\ m^{-2}\ year^{-1}$; Dittmar et al. 2001). The difference was attributed to the fact that small-scale studies usually do not account for the gradual release of DOC from detritus suspended or floating in offshore waters (Kristensen et al. 2008). Off Brazil, Dittmar and his colleagues (Dittmar et al. 2001, 2006; Dittmar and Lara 2001a, b; Schories et al. 2003) found that $13\,mol\ C\ m^{-2}\ year^{-1}$ is exported as detritus from tidal creeks and well-developed forests, with an additional $3\,mol\ C\ m^{-2}\ year^{-1}$ exported as smaller particles and $4\,mol\ C\ m^{-2}\ year^{-1}$ exported as DOC; the combined export equates to about 40% of total litterfall. Of the total export of $20\,mol\ C\ m^{-2}\ year^{-1}$, roughly 60% is eventually transported further offshore in the form of DOC derived from further reworking of particulate matter across the continental shelf. From these data we can estimate a global DOC export from mangroves of $14\,Tg\ year^{-1}$.

DOC exported from mangrove estuaries has a unique chemical signature, derived from degradation products of mangrove detritus incorporated into the soil and often seeping out of the porewater (Section 5.2); the origin of this DOC is often deduced from a clear tidal signature, with mangrove DOC leaving the estuary during the ebb tide and DOC of marine origin entering the estuary during the flood tide (Bouillon et al. 2003, 2007b, c). Thus, most of the DOC exported does so by way of tidally-induced porewater flow (Schories et al. 2003).

Most of the DOC is refractory to immediate microbial, physical, and photochemical decay. In a detailed study of the decomposition of plant-derived

DOM along a seaward gradient in the Florida Everglades, Scully et al. (2004) observed that polyphenolic compounds are degraded mainly via photolysis and that high molecular weight compounds are degraded primarily through microbial and physicochemical processes. These latter processes initiate the formation of refractory, highly colored, high molecular weight polymers. Thus, there is some rapid degradation of mangrove-derived DOC followed by much slower transformation of DOM. This finding is similar to that found by Maie et al. (2008) for DON compounds in mangrove and coastal waterways. A high proportion of tannins precipitate upon exposure to salt and also by sorption to sediments in the estuary. Some DON co-precipitates with the tannins, and these complexes are highly reactive, with a half-life in the water-column of <1 day. Proteins are released gradually from these DON-tannin mixtures, so tannins play an important role in retaining nitrogen in the system, buffering the loss of N through the prevention of rapid tidal export (see Section 4.2).

Although there is a clear pattern of export from mangroves, what role this material has as a nutrient subsidy for offshore food webs is unclear. A picture is emerging, however, which indicates that the extent of mangrove influence is normally restricted to a few kilometers offshore (Lee, 1995; Alongi 1998; Baltzer et al. 2004) where seagrass beds and coral reefs can be supplemented by DIC derived from mangrove respiration (Jennerjahn and Ittekkot 1997; Ovalle et al. 1999; Machiwa 2000; Machiwa and Hallberg 2002; Mfilinge et al. 2005; Bouillon et al. 2008). DOC is often transported further offshore than particulate material, especially from mangroves lining large deltas such as the Amazon (Dittmar et al. 2001). This material, in fact, has been chemically traced to the edge of the continental margin.

The limited impact of mangrove detritus on offshore food webs can be attributed to several factors:

- Local geomorphology and hydrodynamics of mangrove estuaries mitigates against extensive outwelling of labile material.
- The presence of coastal boundary zones off tropical coasts or a high salinity plug in the dry season can efficiently trap litter and suspended particles inshore.
- Most material lost from the system is either highly refractory particulate matter or DOC, the labile fraction of which can be considerably degraded further in the water-column.

These generalizations do not hold so well for large river systems such as the Amazon and Indus.

Recent studies of water-air CO_2 fluxes from mangrove waterways and adjacent inshore waters suggest that pelagic mineralization of organic matter and subsequent emission of CO_2 to the atmosphere could represent another significant pathway of carbon export from mangrove ecosystems (Ghosh et al. 1987; Richey et al. 2002; Borges et al. 2003; Bouillon et al. 2003, 2007a–c; Biswas et al. 2004; Barnes et al. 2006; Ramesh et al. 2007; Upstill-Goddard et al. 2007; Koné and Borges 2008; Ralison et al. 2008). These studies consistently found that mangrove waters are oversaturated in CO_2 as a direct result of pelagic respiration and CO_2 respired within the forest soils that is dissolved in the porewater and transported laterally

by tidal pumping to the adjacent creeks and waterways (Borges et al. 2005). Flux rates, measured either using flux chambers or by modelling air–sea exchange, vary greatly with tidal stage, temperature, precipitation, and location. The Sunderbans bordering the Bay of Bengal, where mangroves constitute nearly 3% of the world's total mangrove area, contributes greatly to the control of CO_2 exchange between air and sea. Measuring diurnal and seasonal variations of CO_2 exchange, Biswas et al. (2004) found that in the post-monsoon months CO_2 saturation and fluxes are minimal and maximal in the pre-monsoon and early monsoon months; the waters of the Sunderbans are heterotrophic throughout the year. The Sunderbans mangrove forest emits $314.6\,\mu$mol C m^{-2} day^{-1} of CO_2 to the atmosphere even though nearly 60% of CO_2 emitted by the ecosystem is removed from the atmosphere by biological processes (e.g., plant uptake).

Averaging the data in Table 6.2 gives a mean flux rate of 43.3 mmol C m^{-2} day^{-1}. Using a higher mean rate of 72 mmol C m^{-2} day^{-1}, Koné and Borges (2008) estimated that CO_2 emission from mangrove waters corresponds to ≈7% of the total emission from oceanic waters at subtropical and tropical latitudes, and about 24% of the total CO_2 emissions from coastal waters globally. The percentage contribution by mangrove waters to global emissions will change as more measurements are made, but these preliminary estimates indicate that, like organic carbon, the mangrove contribution of inorganic carbon to the global ocean is disproportionate to their relatively small area.

Table 6.2 Rates of water–air exchange of CO_2 (mmol C m^{-2} day^{-1}) from mangrove waters

Location	Flux	Reference
Saptamukhi Creek, India	56.7 ± 37.4	Ghosh et al. 1987
Mooringanga Creek, India	23.2 ± 10.1	Ghosh et al. 1987
Itacuraçá Creek, Brazil	113.5 ± 104.4	Ovalle et al. 1990, Borges et al. 2003
Florida Bay, USA	4.6 ± 5.4	Millero et al. 2001
Mekong, Vietnam	42.1	Richey et al. 2002
Amazonas, Brazil	175.2	Richey et al. 2002
Nagada Creek, Papua New Guinea	43.6 ± 33.2	Borges et al. 2003
Gaderu Creek, India	56.0 ± 100.9	Borges et al. 2003
Norman's Pond, Bahamas	13.8 ± 8.3	Borges et al. 2003
Godavari, India	21.9 ± 26.1	Bouillon et al. 2003
Tidal Creeks, Godavari	70.2 ± 127.0	Bouillon et al. 2003
Kakinada Bay, India	8.3 ± 13.6	Bouillon et al. 2003
Sunderbans, India	3.2	Biswas et al. 2004
Ras Dege, Tanzania	33	Bouillon et al. 2007c
Adyar, India	17.8	Ramesh et al. 2007
Muthupet, India	31.8	Ramesh et al. 2007
Pichavarum, India	6.1	Ramesh et al. 2007
Shark River, Florida	43.8 ± 52.1	Koné and Borges 2008
Ca Mau, Vietnam	94.2 ± 50.9	Koné and Borges 2008
Betsiboka estuary, Madagascar	9.1 ± 14.2	Ralison et al. 2008

6.2.2   Dissolved Nitrogen and Phosphorus Exchange

The net direction of dissolved nutrient exchange between mangrove waterways and the adjacent coastal zone depends upon tidal range, extent of groundwater discharge (Section 3.3), ratio of evaporation to precipitation, rates of primary productivity, salinity, turbidity, pH, dissolved oxygen concentrations, and rates of microbial assimilation. Another driving force often overlooked is the extent to which porewater concentrations of nutrients exceed the demands of primary producers (Dittmar and Lara 2001c). Simply, a system will tend to export nutrients if there are more nutrients than needed for utilization within the ecosystem. Conversely, nutrients such as nitrogen will be imported into the system if there is not enough available. Anthropogenic changes sustained by estuaries may also lead to shifts in patterns of nutrient and material exchange. In the Red River estuary of Vietnam, where there has been a massive increase in mangrove production due to large-scale accumulation of sediments transported from upriver, the estuary has become a sink for N and P and this pattern is directly attributable to the increase in mangrove forests (Wösten et al. 2003).

Some nutrient species are imported while others can be exported from the same ecosystem (Table 6.3). For instance, Coral Creek in the Missionary Bay ecosystem, exports significant quantities of litter and some nitrate, but imports phosphate, silicate, ammonium, and DON (Boto and Wellington 1988; Alongi 1996). Some estuaries located in the wet tropics exhibit strong outwelling patterns (Ovalle et al. 1990; Ayukai et al. 2000; Mukhopadhyay et al. 2006); nearly all ecosystems exhibit seasonality of such patterns related to local weather, such as extended drought or intense storms. In short, there are no universal patterns of dissolved nutrient exchange between mangroves and adjacent coastal waters, even if the same ecosystem outwells particulate material.

Table 6.3 Net annual exchange of dissolved nutrients (mmol m^{-2} $year^{-1}$) for various mangrove estuaries worldwide. I = import, E = export

Location	NH_4	NO_3	PO_4	DON	Reference
Coral Creek, Australia	I	E	I	I	Boto and Wellington 1988
Sepetiba Bay, Brazil	E	E	E		Ovaille et al. 1990
Klong Ngao, Thailand		I	I		Wattayakorn et al. 1990
Estero Pargo, Mexico	I	I		E	Rivera-Monroy et al. 1995a
Conn Creek, Australia		E	E		Ayukai et al. 1998
Sawi Bay, Thailand	E	E	E		Ayukai et al. 2000
Taylor River, Florida	I	E			Davis et al. 2001
Bandon Bay, Thailand	E	E	E		Wattayakorn et al. 2001
Gazi Bay, Kenya	E	E	E		Mwashote and Jumba 2002
Okinawa, Japan	E	I			Kurosawa et al. 2003
Red River, Vietnam	I	I	I		Wösten et al. 2003

6.3   Carbon Balance in Mangrove Ecosystems

The balance between photosynthetic gains by plants and respiratory losses by all organisms is reflected in the exchange of carbon between the ecosystem, atmosphere, and the adjacent coastal ocean. This balance is called net ecosystem production (NEP) or net ecosystem exchange (NEE). NEP has become a crucial characteristic in ecosystem assessments of whether or not anthropogenic increases in atmospheric CO_2, resulting from fossil fuel combustion and the clearing of forests, has altered the carbon balance. Forests are particularly important storage sites for CO_2, reducing the impact of human inputs into the atmosphere (Perry et al. 2008).

Determining the carbon balance of a mangrove ecosystem is similar to that for an individual tree (see Section 2.5.2) in that carbon inputs from photosynthesis must be balanced by losses such as respiration and the shredding of leaves. At the ecosystem level, however, other inputs and outputs must be accounted for, such as groundwater, burial within the forest floor, tidal exchanges, river inputs, and respiratory losses from microbes, fauna, and flora. In disturbed ecosystems, human impacts also have to be accounted for, such as losses due to logging, clear felling, fishing, and gains from aquaculture and sewage. These inputs and outputs are needed to construct mass balance models to estimate net ecosystem production. But first, we will look at a more holistic approach to quantifying mangrove carbon balance.

6.3.1   Whole-Ecosystem Balances

Techniques borrowed from micrometeorology and terrestrial ecology have provided a new approach to measuring the exchange of CO_2 between forests and the atmosphere (Aber and Melillo 2001; Perry et al. 2008). One approach, the eddy covariance method, estimates the net exchange of CO_2 by measuring the vertical gradients of CO_2 from the forest floor to above the canopy (Fig. 6.1). With simultaneous measurements of wind speed, wind direction, and air temperature, the vertical CO_2 profile can be used to estimate carbon flux in and out of the forest over various time intervals.

The eddy covariance method captures the movement of air through the canopy which occurs as a rapidly oscillating set of eddies or irregular pockets of turbulent air shifting in response to the interaction between winds and the vortices induced by the presence of the foliage. Net carbon accumulation is occurring if the air moving out of the canopy has a lower CO_2 concentration than the air moving into the forest.

The first studies to use this method in mangroves were conducted by Monji and his colleagues (Monji et al. 1996, 2002a, b; Monji 2007) at Phangnga in southern Thailand. Using several different gradient analyses (due to problems measuring CO_2 concentrations during heavy rainfall and from both wet and dry soils), Monji et al. (2002a, 2000b) found that, as expected, there are clear diurnal changes in CO_2 flux above the canopy (Fig. 6.2) with turbulent CO_2 flux showing net uptake during
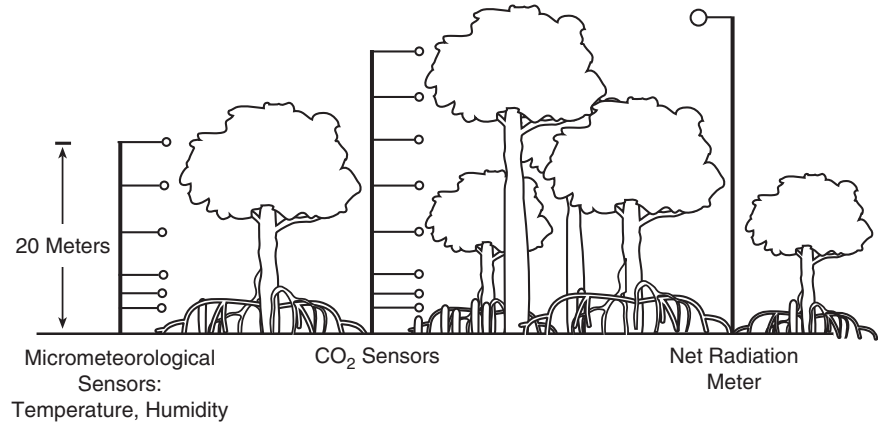
Fig. 6.1 Arrangement of the instrumentation and measurements needed to quantify the vertical gradient of CO_2 in a mangrove forest using the eddy covariance approach
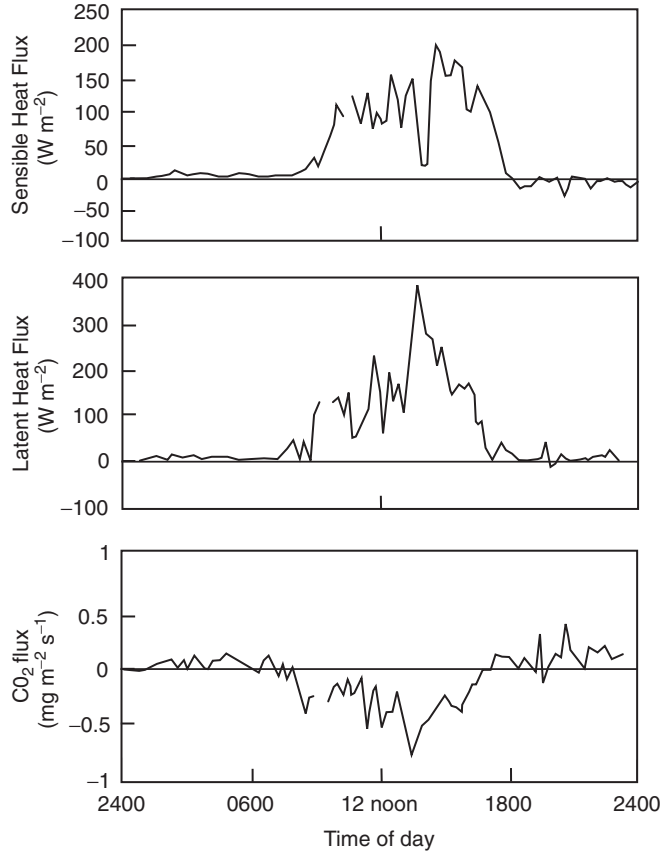

Fig. 6.2 Diurnal fluxes of sensible heat, latent heat, and CO_2 over the Phangnga mangrove forest of southern Thailand on 9 September 1998 (Modified from Monji et al. 2002a)

daytime (shown as a negative flux) and net flux out of the forest at night (a positive flux); this pattern is mirrored in the sensible and latent heat fluxes (Fig. 6.2). Heat energy mirrors gas flux because energy is used for the work of photosynthesis and respiration; latent heat is the energy transferred between the forest and the atmosphere by water evaporation or the condensation of water vapor, whereas sensible heat is the energy transferred between the forest and the atmosphere by conduction and movement by convection.

Soil respiration was an order of magnitude smaller than CO_2 flux from the canopy, with CO_2 flux not significantly different between wet and dry seasons in these Thai forests (Monji et al. 2002a, b). Net CO_2 flux averaged 0.11 mg m^{-2} s^{-1}. This equates to a net ecosystem production (excluding any tidal losses) of 78.8 mol C m^{-2} year^{-1} and for the entire mangrove ecosystem at Phangnga (30,000 ha) of 23.6 Gmol C year^{-1}. A similar study conducted in the Sunderbans mangrove forest ecosystem bordering the northern Bay of Bengal (Ganguly et al. 2008) measured heat and gas fluxes over the course of a year. Ganguly et al. (2008) found a seasonal pulse of CO_2 flux, with lower rates of daytime flux during the wet monsoon (Fig. 6.3) which was attributed to cooler temperatures, a decline in salinity, and less solar radiation. Nighttime fluxes did not vary seasonally (Fig. 6.3) but the total CO_2 exchange was 121 mol C m^{-2} year^{-1} for a total net ecosystem production for the Sunderbans (426,400 ha) of 515.9 Gmol C year^{-1}.

6.3.2 The Mass Balance Approach

The mass balance approach is a less recent and arguably more laborious (and expensive) method of estimating carbon balance and net ecosystem production. This approach is based on the simple premise that the flow of carbon in an ecosystem is in steady-state. A simple mass balance equation is the basis for the flux of
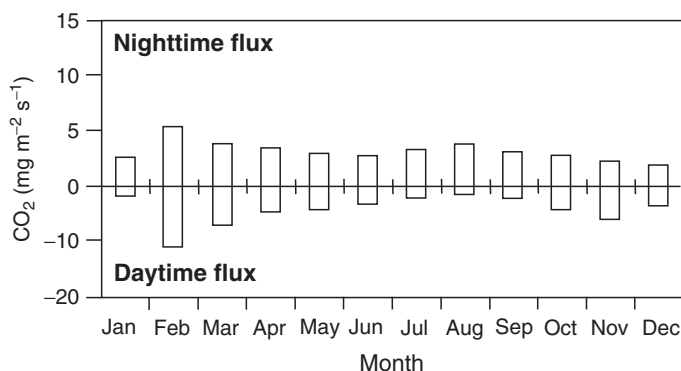

Fig. 6.3 Monthly variation of CO_2 flux during the day and at night over the Sunderbans mangrove forest. Vertical bars represent mean flux rates. (Modified from Ganguly et al. 2008)

carbon (or any other element), $C_i = F_i + \Sigma R_i$, where C_i = concentration of element i in mass per unit volume per unit time; F_i = flux of element i in mass per unit area or volume per unit time; R_i = rates of each physical, chemical or biological process affecting element i in mass per unit volume or area per unit time. Simply, the equation represents the difference between what carbon comes in and what carbon goes out. In ecological terms, when carbon that comes in or is produced (total input) exceeds what carbon goes out or is consumed (total output), net ecosystem production is greater than zero and the system is accumulating carbon. If it roughly equals zero, the system is in steady-state and if negative, the ecosystem is losing more carbon that it is gaining. Whether or not ecosystems are in positive or negative balance has important consequences for ecosystem sustainability, as we will discuss in Section 6.7.

Mainly because so many separate measurements are involved, only six mangrove ecosystems have been studied sufficiently to enable preliminary mass balance estimates of carbon to be made: Rookery Bay in Florida, the Matang Mangrove Forest Reserve in Malaysia, Sawi Bay in Thailand, and Hinchinbrook Channel, Missionary Bay, and Darwin Harbour in northern Australia.

A few characteristics of carbon flow in these six ecosystems warrants analysis (Table 6.4): (1) these mangrove ecosystems are net autotrophic, with an average P_G/R ratio of 1.6, higher than the Gattuso et al. (1998) estimate of 1.4, and (2) gross primary production and net ecosystem production average 383 and 139 mol C m^{-2} year^{-1}, higher than the Gattuso estimates of 232 and 89 mol C m^{-2} year^{-1}, respectively. Despite the obvious drawbacks of such budgets, it is clear that:

- These ecosystems export organic carbon equivalent to 2-25% of mangrove net primary production.
- Canopy respiration equates to 58% of gross primary production and is probably higher as the data account only for respiration of leaves and do not include stem and root respiration.
- Mangrove production dominates carbon input, but inputs from human settlements and activities, and from riverine and oceanic contributions, can be substantial as exemplified in the Matang Mangrove Forest Reserve, Hinchinbrook Channel and Darwin Harbour ecosystems.
- Soil and water-column respiration losses pale in comparison to canopy respiration.
- There is proportionally little carbon burial within the forest floor, ≈ 1–4% of total organic carbon input to the forest.
- Net ecosystem production (NEP) is positive in all six ecosystems, but true NEP is probably lower because losses of CO_2 from the water to the atmosphere were not measured at any of these locations.

The differences between these estimates and those of Gattuso et al. (1998) are undoubtedly due to the dominance of Australasian ecosystems in the present calculations. These ecosystems are likely to be among the more productive mangroves in the world. Further, some values in Table 6.4 represent only a few measurements, so the results must be treated cautiously as there is large error in many of the numbers.

Table 6.4 Physical characteristics and mean rates of organic carbon inputs and outputs for the Rookery Bay (RB), Matang Mangrove Forest Reserve (MMFR), Sawi Bay (SB), Hinchinbrook Channel (HC), Missionary Bay (MB) and Darwin Harbour (DH) mangrove ecosystems. Units are mol C m−2 year−1, unless noted otherwise. Data from Twilley (1985b, 1988), Caffrey (2003), Clough et al. (1997b), Clough (1998, unpublished data), Gong and Ong (1990), Ayukai and Miller (1998b), Ayukai et al. (1998, 2000), Alongi (1998), Alongi et al. (1998, 1999, 2000c, 2001, 2004a), Tanaka and Choo (2000), Alongi and McKinnon (2005), Burford et al. (2008).

	RB	MMFR	SB	HC	MB	DH
Percentage of mangrove area to total ecosystem area	24%	67%	20%	36%	39%	18%
Tidal range (m)	0.55	2.0	1.3	2.4	2.3	7.8
Rainfall (m year−1)	1.3	2.5	1.2	2.5	2.5	2.2
Sources						
Mangrove GPP	276.5	415.3	450.4	370.3	294.0	490.2
Algal GPP	68.5	69.2	16.1	16.6	16.4	49.9
Other inputs[a]	NA	23.2	0.1	15.8	NA	42.0
Total inputs	345.0	507.7	466.6	402.7	310.4	582.1
Sinks						
$Resp_{canopy}$	184.9	293.2	297.1	190.3	158.0	201.8
$Resp_{water}$	114.0	11.5	24.3	8.5	8.2	10.5
$Resp_{soil}$	16.4	36.1	26.7	9.4	10.7	53.6
Burial	NA	9.4	22.9	5.6	4.2	NA
Export and other outputs[b]	5.3	30.5	5.9	10.4	27.7	26.7
Total outputs	320.6	380.7	354.0	224.2	208.8	292.6
NEP[c]	24.4	127.0	112.6	178.5	101.6	289.5
%NEP/GPP	9%	31%	25%	48%	35%	59%
%NEP/NPP	27%	100%	73%	100%	75%	100%
P_G/R	1.09	1.42	1.34	1.86	1.75	2.03
% TOC input buried	NA	2%	4%	1%	1%	NA
% Export of mangrove NPP	6%	25%	2%	6%	20%	9%

[a]Net river and oceanic inflow, aquaculture wastes, sewage, seagrass production.
[b]Logging, net river and oceanic inflow, aquaculture wastes, sewage.
[c]Total Inputs minus Total Outputs.

Further, both Rookery Bay and Darwin Harbour represent outliers at both extremes of tidal range and are not typical of other mangrove estuaries, most of which reside in more moderate (1–3 m) tidal conditions.

What regulates organic carbon fluxes at the ecosystem level? Physiological constraints and physicochemical conditions control growth and production of individual populations and communities, but why does net ecosystem production, for example, vary so much among these six ecosystems? Characteristics unique to each ecosystem play some role. In the Matang Reserve, large tracts of the forest are sustainably clear-felled for fuel and charcoal, and there are less well-regulated aquaculture activities and organic pollution within the reserve. In Sawi Bay, most of the forests are <25 years old, as many stands have been restored after unregulated logging for pond aquaculture in the 1980s and for industrial developments in the 1970s.

A plot of the relationship between tidal range and net ecosystem production (Fig. 6.4) for these six ecosystems suggests that tides play an important role in regulating ecosystem production. This idea supports the tidal subsidy hypothesis originally exposed by the Odum's (Odum 1968, 2000; Odum et al. 1979, 1995) and by Nixon (1988). Odum et al. (1995) suggested that maximum power is achieved when biological 'pulses' are in synchrony with external pulses such as tides. A comparative analysis of lake and marine ecosystems led Nixon (1988) to argue that the additional mechanical energy from tides has important consequences for differences in functioning between freshwater and marine systems, including more intensive fisheries yield, stronger currents, and more vigorous vertical mixing. These physical factors are linked to tides, assisting in maximizing transport of wastes and toxic materials from the ecosystem, assisting in oxygenating soils that would otherwise be waterlogged, and maintaining an intermediate level of disturbance in breaking down biological, chemical, and physical gradients within estuaries. Such suppositions may serve to explain the positive relationship between tidal range and mangrove net ecosystem production.

A contrary hypothesis is that these values do not necessarily reflect net ecosystem production, but in fact represent losses of respired carbon not measured in these ecosystems. As we will discuss in Section 7.1, much carbon from soil respiration may be unaccounted for, lost via lateral transport or via groundwater flow, pathways that were not measured in these ecosystems. The large tidal range in Darwin Harbour, for example, may translate into greater lateral transport of respired carbon in the intersti-
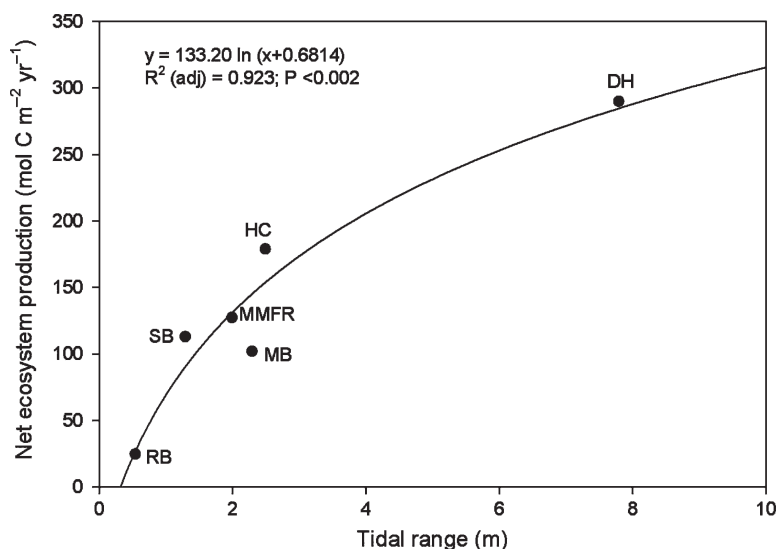

Fig. 6.4 The relationship between tidal range and net ecosystem production in various mangrove estuaries. (Data from Table 6.4). DH = Darwin Harbour, HC = Hinchinbrook Channel, MB = Missionary Bay, MMFR = Matang Mangrove Forest Reserve, SB = Sawi Bay, and RB = Rookery Bay

tial water from the forest floor; hence, what would appear to be greater NEP than in the ecosystems with smaller tides, may in fact be a greater proportion of carbon lost from the ecosystem. If true, this means that mangroves are contributing even greater amounts of dissolved inorganic carbon to the tropical coastal ocean (see Section 7.1).

6.4 Nitrogen Flow Through Mangrove Ecosystems: The Hinchinbrook Island Study

There is only one mangrove ecosystem for which a complete nitrogen budget exists: the mangroves of Missionary Bay at the northern end of Hinchinbrook Island in north Queensland, Australia (Fig. 6.5). The budget for this ecosystem was first presented in 1992 (Alongi et al. 1992), and except for some additional data and corrections, the initial conclusions remain valid. Nevertheless, it is instructive to update the budget and reiterate the conclusions here as they have greater relevance now as mangroves are becoming increasingly impacted by anthropogenic inputs.
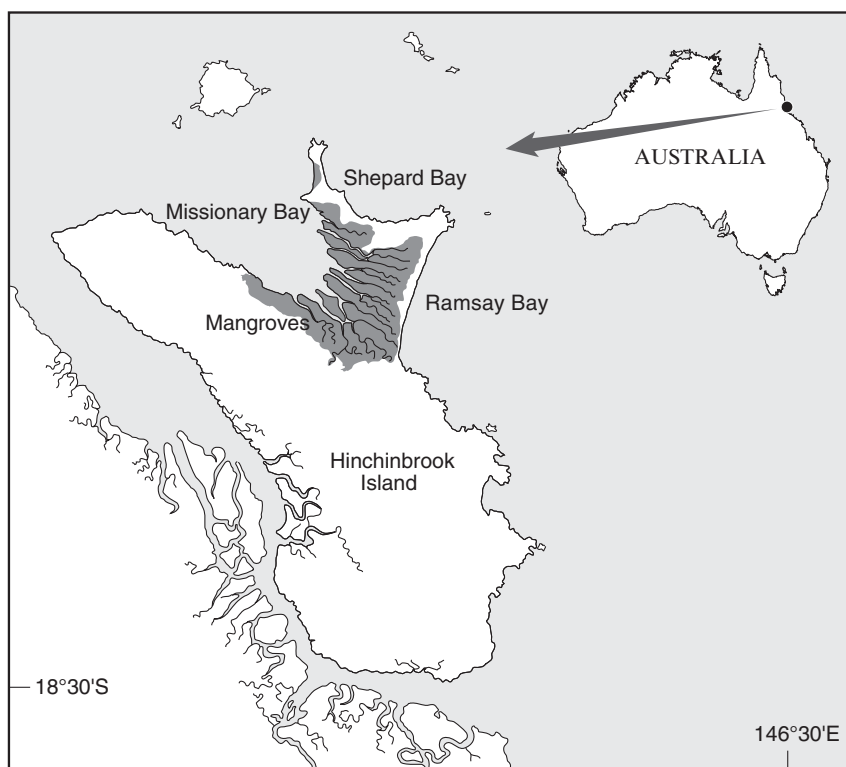

Fig. 6.5 Location of Hinchinbrook Island and the mangroves of Missionary Bay in relation to the Queensland coast

Hinchinbrook Island (18°20' S, 146°10' E) is a heavily forested and mountainous island that is a national park, situated adjacent to the Australian mainland about 100 km NW of the city of Townsville. The western boundary of the island is separated from the mainland by Hinchinbrook Channel, a narrow waterway 50 km long and lined with extensive, deltaic mangrove forests. At the northern boundary is located Missionary Bay (64 km^2), consisting of a series of finger-like projections of mangrove forests separated by tidal creeks. The entire mangrove area is 42.5 km^2, composed mostly of mixed *Rhizophora* spp. Total water volume exchanged over an average tidal cycle is approximately 1.5×10^7 m^3; tides are semi-diurnal with an average range of 2.3 m. Although the Missionary Bay mangroves receive an average annual rainfall of 2,500 mm, there is no significant groundwater input. It is a fully marine system. Even during the summer wet season, salinity rarely dips below 33.

The main pathways for nitrogen to enter the system are: (1) nitrogen fixation by microbial consortia residing on surface soils, logs, other pieces of fallen timber, and live tree stems and above-ground roots, (2) tidal exchange, and (3) precipitation (Table 6.5). The estimate for groundwater represents the amount of rainwater falling within the mountainous barrier bordering the mangroves and assumes that all of this water runs down to the mangroves. Tides bring in mainly DON with lesser amounts of ammonium, nitrate and nitrite, but no particulate nitrogen.

Net tidal exchange represents losses due mainly to the export of litter (Table 6.5) which constitutes the main loss of nitrogen from the system, followed by denitrification and to a lesser extent, sedimentation in the forest and on creek banks. The outwelling of particulate and dissolved nitrogen is clearly the dominant process. Other possible sources and sinks remain unquantified, such as volatilization of ammonium, and migration of fish, prawns, birds, and bats, but these losses are probably small and unlikely to significantly alter the net balance of nitrogen.

Net tidal exchange is 97 Kmol N year^{-1}. Considering the extrapolations made and the systematic and relative errors involved with so many different individual measurements over time, the budget is in overall balance. Considering that the net ecosystem production is estimated at 4,318,000 Kmol C year^{-1} (Table 6.4), it is clear that nitrogen is greatly conserved within this ecosystem.

A number of mechanisms operate to conserve nitrogen. First, there is a very high rate of N cycling within the soil, to the extent that the bulk of dissolved nitrogen is taken up by the trees; as noted in Chapter 5, comparatively little (about 5% of total N input to the soil) is lost via denitrification and by efflux during flood tides. The microbe–soil–root complex thus rapidly recycles nitrogen (and other nutrients) via mortality, decomposition, uptake, and growth of organisms, thus serving as a retention mechanism. Second, crabs assist in minimizing the loss of litter and maximizing N gain by their activities in the soil. Third, tree stems, roots, logs, and other mangrove timber on the forest floor provide space to maximize colonization of nitrogen-fixers and thus the rate of atmospheric input. Finally, the C:N ratio of dissolved and particulate material leaving the forest is higher than Redfield and high in concentrations of refractory compounds such as humic and fulvic acids, and polyphenolics, indicative of an advanced state of decomposition. In short, little that is biologically labile leaves the forest and its waterways.

Table 6.5 Nitrogen budget (kmol N year^{-1}) for the mangrove ecosystem in Missionary Bay, Australia. The budget was constructed using data, including habitat areas, from papers cited on page 279 in Alongi et al. (1992)

Process	Input	Output	Net exchange
Precipitation			
$NO_2 + NO_3$	0.7		
NH_4^+	0.5		
DON	1.3		
Particulate N	0.1		
			2.6
Groundwater			
	2.4		
			2.4
Nitrogen fixation			
Saltpan	466.2		
Soil surface	479.7		
Prop roots	1,192.7		
Logs/timber	930.7		
Stem	376.7		
			3,446
Tidal exchange			
$NO_2 + NO_3$	437.5	525.0	−87.5
NH_4^+	928.0	696.8	231.2
DON	12,684.3	8,821.4	3,862.9
Particulate N		6,360.8	−6,360.8
Denitrification			
		658.4	−658.4
Sedimentation			
		342.5	−342.5
Total	17,501	17,405	95.9

As no other mangrove ecosystem has been explored in sufficient detail to enable construction of a nitrogen budget, comparisons with other mangroves are limited to specific processes. For instance, in the Fukido mangroves on Okinawa (Kurosawa et al. 2003), export of nitrogen was measured as 0.17 mmol N m^{-2} day^{-1} roughly equivalent to accumulation of nitrogen in the soil (0.2 mmol N m^{-2} day^{-1}). In this ecosystem, both export and accumulation each equaled only about 5% of gross primary production. In the Potengi mangrove forests of northern Brazil (Silva et al. 2007), export of N was estimated at 0.3 mmol N m^{-2} day^{-1}, and like the Fukido mangroves, this export constituted only a small percentage of mangrove production.

One process that has only recently been measured from mangrove ecosystems is the loss of ammonia gas. This process was assumed to be relatively insignificant in Missionary Bay, but a thorough study of ammonia exchange in the Sunderbans suggests otherwise (Biswas et al. 2005). Emission of ammonia gas from the forests to the atmosphere averages 1,790 kgN km^{-2} year^{-1} but wet and dry inputs average 2,350.5 kg N km^{-2} year^{-1} and there is net import of ammonia to the waterways on the order of 775.7 kg N km^{-2} year^{-1}. If one applies these rates to Missionary Bay,

there would be a total input of 7,910.7 kmol N year^{-1} and total output of 5,434 kmol year^{-1} for a total net ammonia exchange of nearly 2,500 kmol N year^{-1}, which would be the second largest flux after DON exchange (Table 6.5).

As indicated by Alongi (1998), there are a few insights to be learned from comparing the nitrogen budget of Missionary Bay and the nitrogen budget for the Great Sippewissett salt marsh located on the western shore of Cape Cod, Massachusetts. We can how update this information and add the nitrogen budget for another salt marsh, the Sapelo Island ecosystem, located on the Georgia coast (Table 6.6). There are a number of similarities between the mangroves and salt marshes:

- Tides dominate physical control of nutrient exchange.
- There is an overall balance between inputs and outputs, considering magnitude of errors.
- Tidal import and nitrogen fixation are the major inputs.
- Tidal outwelling is the major output.

But there are a number of striking differences:

- Nitrogen derived from freshwater is proportionally smaller in Missionary Bay.
- Tidal export as a percentage of total output is greater in Missionary Bay.
- Denitrification is a greater proportion of total output in the Great Sippewissett (12%) and Sapelo Island (25%) marshes than in the mangroves (4%).
- Rates of nitrogen fixation exceed denitrificatiion in Missionary Bay, but the reverse is true in the salt marshes.
- Sedimentation rates are confounded between ecosystems, with Missionary Bay and Sapelo Island having proportionally small (1–2% of total output) burial rates compared with Great Sippewissett marsh (12%).
- There is little particulate input into Missionary Bay, but there is significant import of particulate nitrogen into both salt marshes.

Table 6.6 Comparison of nitrogen budgets (kg N year^{-1}) of the Australian mangrove and American salt marsh ecosystems (Data from Table 6.5, Valiela and Teal 1979; Whitney et al. 1981; Thomas and Christian 2001). NA = not available

	Missionary Bay, Queensland, Australia	Great Sippewissett, Massachusetts, USA	Sapelo Island, Georgia, USA
Inputs			
Precipitation	36	271	3,480
Groundwater	34	6,435	464
N$_2$ fixation	48,244	1,642	212,052
Tidal import	196,697	21,833	740,560
Other	0	20	NA
Total inputs	245,011	30,201	956,556
Outputs			
Tidal export	229,656	26,316	762,352
Denitrification	9,218	4,349	261,864
Sedimentation	4,795	4,150	15,086
Other	0	30	NA
Total outputs	243,669	34,845	1,039,302
Net exchange	+1,342	−4,644	82,746

It is unlikely, however, that such differences and similarities in nitrogen flow will hold true in any future comparisons between mangroves and salt marshes. Other mangroves and salt marshes are undoubtedly different, and it is exceedingly likely that such comparisons will find differences among mangrove ecosystems as great as those between mangroves and salt marshes. We do not have sufficient understanding of the inherent functional characteristics of each ecosystem type, as more ecosystem-level budgets are urgently needed to redress this discrepancy.

6.5 Mineral Cycling

With the exception of some data detailing element concentrations in soil and tree components, little information is available on cycling of essential elements such as iron, potassium, sodium, magnesium, calcium, zinc, copper, manganese, and vanadium, in mangrove ecosystems. Work in Chinese mangroves by Lin Peng and his colleagues (Li 1997; Lin 1999) have established turnover times of various elements via litterfall. Litter represents only a small part of the cycling of matter in a mangrove forest, but these extensive studies offer a glimpse of variations in turnover times among species and elements (Fig. 6.6). The turnover times of potassium, calcium, and sodium are shorter in *Kandelia candel* forests than through the litterfall of *R. stylosa* and *B. sexangula* forests. Importantly, these data suggest that turnover of these elements
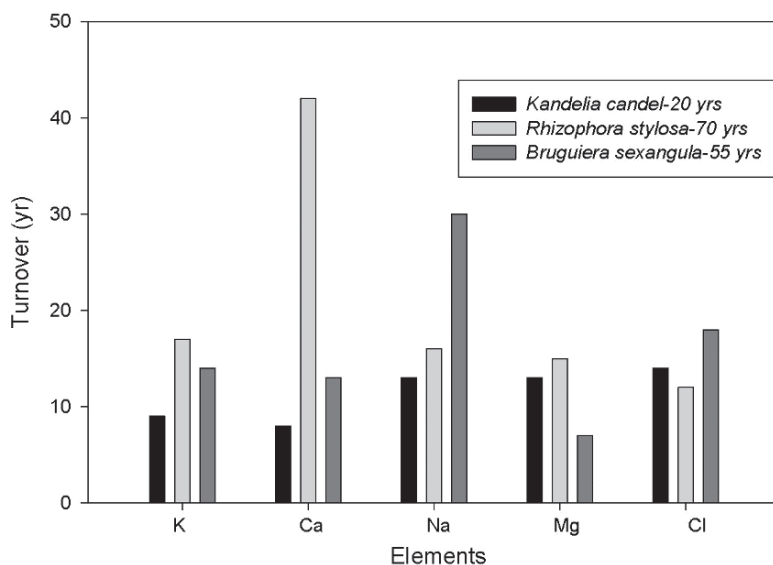

Fig. 6.6 Turnover time of potassium, calcium, sodium, magnesium, and chlorine as throughput via litterfall in three mangrove forests of different species and age in southern China (Data from Lin 1999)

Table 6.7 Turnover times (years) of soil elements in four mangrove forests of different age in southern Thailand (Modified from Alongi et al. 2004b)

	25 year-old R. apiculata	5 year-old R. apiculata	3 year-old R. apiculata	3 year-old C. decandra
Forest production (t C ha^{-1} year^{-1})→	52.8	16.9	37.0	22.9
Element				
N	4	13	12	16
P	6	26	13	22
S	113	642	322	169
Fe	916	21,272	18,264	23,098
Na	6	43	36	50
Mg	9	85	81	65
K	21	127	64	114
Ca	2	40	8	17
Zn	162	733	505	453
Cu	610	470	147	275
Mn	3	120	14	139
Mo	28	320	430	200

is faster in mangroves, on average, than in many terrestrial forest types (Barnes et al. 1998; Aber and Melillo 2001; Kimmins 2004).

The turnover time of an element most likely relates more closely to the rate of primary production than to forest age. For instance, in mangrove forests aged from 3 to 25 years in southern Thailand, turnover of soil nitrogen, phosphorus, sulfur, iron, sodium, magnesium, manganese, molybdenum, potassium, calcium, copper, and zinc is shorter in the oldest forest, which is also the most productive (Table 6.7). Simply, the greater the rate of carbon fixation, the greater the demand for essential elements. The turnover times in the Chinese mangroves are roughly on the same scale as found in other tropical wetlands and forests (Golley et al. 1975; Dykyjova and Ulehlova 1998; Fassbender 1998). However, complete ecosystem-level budgets of many essential elements are urgently needed to offer insights into element cycling in mangrove forests.

6.6   Systems Analysis: Understanding Links Among Various Functions of an Ecosystem

Systems ecology as nurtured by Howard Odum (1983) has led to the development of conceptual and stimulation models into the behavior of the functioning of ecosystems. Such models are used to highlight gaps in our knowledge and to predict the impact of pollutants and other human disturbances on ecosystems, but they are being used increasingly for economic purposes in the relatively new field of ecological economics. In this section, models depicting various functions of man-

grove ecosystems are assessed in order to understand the use of energetics information in trying to quantify sustainability.

6.6.1 Network Models

The first model of a mangrove ecosystem was conceptual, fostered by the need to clarify new views of trophic interactions and detritus flow (Heald 1969; Odum and Heald 1975). The first true computer simulation model of a mangrove ecosystem was constructed by Ariel Lugo and his colleagues (Lugo et al. 1976). In fact, the original model continues to be improved upon (Pandey and Khanna 1998). In this model, the main pathway of energy flow is the export of detritus from the forest floor to the estuary, with some material being lost through grazing and decomposition, and intercompartmental transfers and interactions modelled as either linear or non-linear functions, depending on the process and assuming steady-state. The model and subsequent sensitivity analysis (Pandey and Khanna 1998) indicates that all variables (detritus, nutrients, mangrove biomass, etc.) are highly sensitive to tidal action, with the most pronounced effect being on the flow of detritus. The strongest influence on mangrove biomass is terrestrial run-off and, secondarily, solar radiation.

An attempt to incorporate modelling of litterfall dynamics into an energy flux budget was first attempted by Wafar et al. (1997) for the mangroves of the Mandovi and Zuari estuaries in west India. They found that mangrove production is important mainly in carbon flow with respect to microbial decomposition, rather than in food chain dynamics directly. Development of computer packages such as NETWORK (Kay et al. 1989) and ECOPATH (Ulanowicz and Kay 1991) has led to use of such models for more sophisticated analysis of flows in mangrove ecosystems (Manickchand-Heileman et al. 1998; Lin et al. 1999; Ray et al. 2000; Wolff et al. 2000; Vega-Cendejas and Arreguin-Sánchez 2001; Ortiz and Wolff 2004; Cruz-Escalona et al. 2007; Ray 2008).

The main premise of these models is to solve a steady-state, mass balance-type equation and to calculate the following network characteristics from the results: the mean length of energy flow pathways, the percentage of recycling (Finn's cycling index, Finn 1976), the extent of connectivity, detritivory, and herbivory among trophic groups, and total system throughout (sum of all energy flows). This is accomplished by balancing the linear equation, $B_i P_i(B_i)^{-1} E_{Ei} - {}^n\Sigma_{j=1} B_j Q_j(B_j)^{-1} D_{Ci} - E_{Xi} = 0$, where B_i = biomass of group i, $P_i B_i^{-1}$ = production/biomass ratio of i, E_{Ei} = proportion of production shunted into predation, B_j = biomass of predator j, $Q_j B_j^{-1}$ = consumption/biomass ratio of predator j, D_{Ci} = fraction of prey i in diet of predator j, E_{Xi} = export of group i.

Use of early versions of ECOPATH resulted in a number of energy flow and trophic transfer models for mangrove-dominated ecosystems. Analysis of Terminos Lagoon in Mexico (Manickchand-Heileman et al. 1998) shows that trophic transfer efficiency is low (7%) but that there is a high degree of recycling (Finn index = 7.0)

and a long average length of food chain paths (10). These results indicate that most energy flow is vested in lower trophic levels. This is despite the fact that early versions of the software did not include bacterial utilization of detritus or possible burial of organic material in sediments; workers at that time were unaware of the preference for benthic algae over detritus by consumers so the model favors the dominance of detrital pathways within the system. In contrast, a balanced trophic model of another lagoon in southwestern Taiwan (Lin et al. 1999) found that high planktonic primary production is the main energy driver of food chains dominated by herbivorous zooplankton. Half of the carbon fixed by phytoplankton is not immediately used by higher trophic levels but shunted into the detritus pool, most of which is directly consumed by fish and other large consumers and eventually exported to intensive fisheries. These fluxes reflect short trophic pathways (mean path length = 3.38) with high trophic transfer efficiencies among the upper trophic groups.

Network analysis of two other coastal lagoons in Mexico (Vega-Cendejas and Arreguín-Sánchez 2001; Cruz-Escalona et al. 2007) indicates intense fisheries productivity, similar to that in Terminos Lagoon, but in one system (Celestun Lagoon) most primary production is exported, as only 4% is grazed and 7% is shunted into the detritus pool. In the other lagoon (Laguna Alvarado) as in Taiwan, net primary production is the main source of energy, with consumption, respiration, and detrital fluxes accounting for 47%, 37%, and 16% of total system throughput, respectively. Clearly, all of these models show that lagoonal-mangrove systems are highly productive, but also point to autotrophs other than mangroves as playing a major trophic role.

In more open, riverine estuaries, modeling of trophic flows supports empirical evidence that mangroves play the major role in energy flow (Wolff et al. 2000). Within the Amazon system, the Caeté tributary possesses one of the world's largest expanses of mangroves, but is subject to intense logging and harvesting of crabs. Modelling of this system has found that shrimp and fish are of relatively low energetic importance (compared with the lower trophic groups) along with mangrove epibenthos, especially crabs such as *Ucides cordatus*, which are heavily harvested. Mean trophic transfer efficiency (10%) and the high gross efficiency of the fishery (catch/net primary production = 9%) is explained by high rates of mangrove logging and crab harvesting. Bacteria contribute 34%, mangroves 19%, fiddler crabs 13%, algae 10%, mangrove crabs 10%, and the remaining trophic groups 14%, of total energy flow. Of greater significance is that the modelling suggests overexploitation of crabs; use of a realistic P:B ratio results in the model not balancing, that is, that more biomass is being harvested than produced. This scenario is a good demonstration of how models can be used to determine the level of sustainable harvesting of resources.

Such models are also of use in determining ecosystem-level differences between pristine and reclaimed mangrove forests. A good example is the work of Santanu Ray and his colleagues (Ray et al. 2000; Ray 2008) in the Sunderbans in India. In an initial network analysis of the benthic food web within the impacted mangroves, Ray et al. (2000) found that herbivorous and detritivorous pathways are equally important, with human impacts resulting in an increase in the relative importance

of algal primary production, herbivorous zooplankton, and meiofauna. Recycling of material is low, but path redundancy is high, suggesting that the benthic communities residing in the impacted mangroves are probably highly resilient to further stress. Further modelling reveals that benthic communities within the virgin forests are typically more detritus-based, being more dependent on litter. The pristine forests have more throughout (539,040 kcal m^{-2} $year^{-1}$) than the reclaimed forests (136,570 kcal m^{-2} $year^{-1}$), indicating more energy is passing through a given area per unit time, but a greater percentage of energy is being lost via respiration in the disturbed forests (Fig. 6.7). Some other clear differences between ecosystems were detected in the network analysis (Fig. 6.7). Relative ascendency, percentage imports and exports, and the Finn cycling index, are all greater in the pristine than in the reclaimed mangroves. This means that the food webs in the reclaimed forests are less organized, but possess communities more capable of replacing each other within a given niche. Also, proportionally more energy is imported and exported from the healthy ecosystem with a greater percentage vested in recycling pathways. It appears that, even with a number of limitations and unsubstantiated assumptions of linearity and steady-state, these models are useful tools for analyzing salient characteristics of how mangroves function as ecosystems.
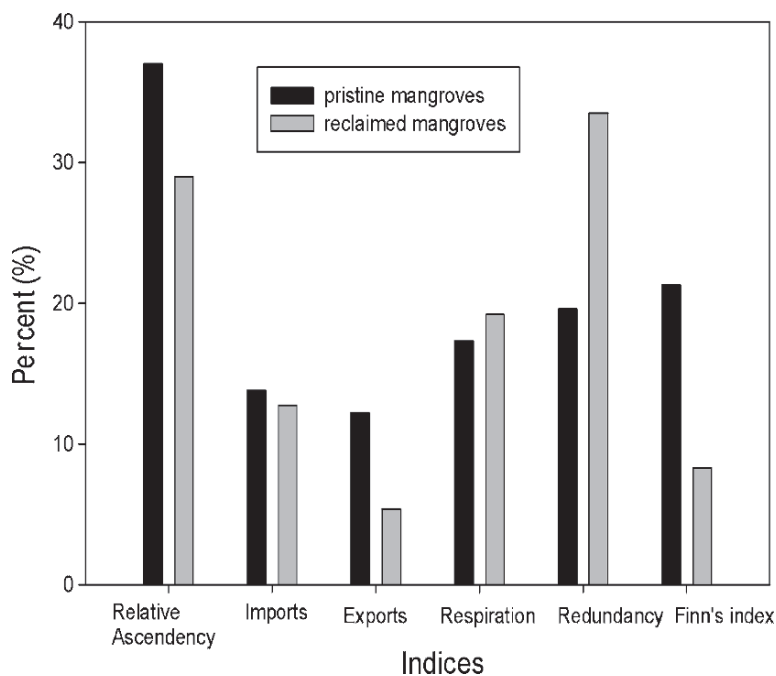

Fig. 6.7 Comparison of some key ecosystem characteristics between pristine and reclaimed mangrove forests in the Sunderbans, India, calculated using network analysis (Data from Ray 2008)

6.6.2   Ecohydrology: Linking Physics and Ecology for Management Applications

Recognizing the links between physical and biological characteristics within eco-systems, and the urgent need to apply ecosystem ecology to management issues, an international meeting sponsored by the International Hydrological Programme of UNESCO developed a rationale and conceptual framework for a new type of model in which hydrological processes are linked to ecological submodels (Zalewski et al. 1997). In the model, a physical submodel divides an estuary into a series of interlinking cells from the mouth to the upper tidal limit of the waterway (Fig. 6.8). The cell at the upper tidal limit receives Q_f, river discharge, sediment (Q_s), detritus, freshwater plankton, and nutrients. The cell at the estuary mouth receives ocean inputs of water, detritus, sediment, nutrients, plankton, and fish. There is a downstream flux resulting from the riverine input through the series of cells and a bidirectional flux from cell to cell depicting tidal mixing, resulting in a turbidity maximum and a limit of oceanic intrusion. There is also either a rate of import or export from every cell from mangroves. These processes are then fit to empirical data and simulated as a series of subroutines using steady-state equations of physical flows and predator–prey interactions.

   The first use of such a model for mangroves was for Darwin Harbour, a large macrotidal estuary sheltering a small city in the Northern Territory, Australia
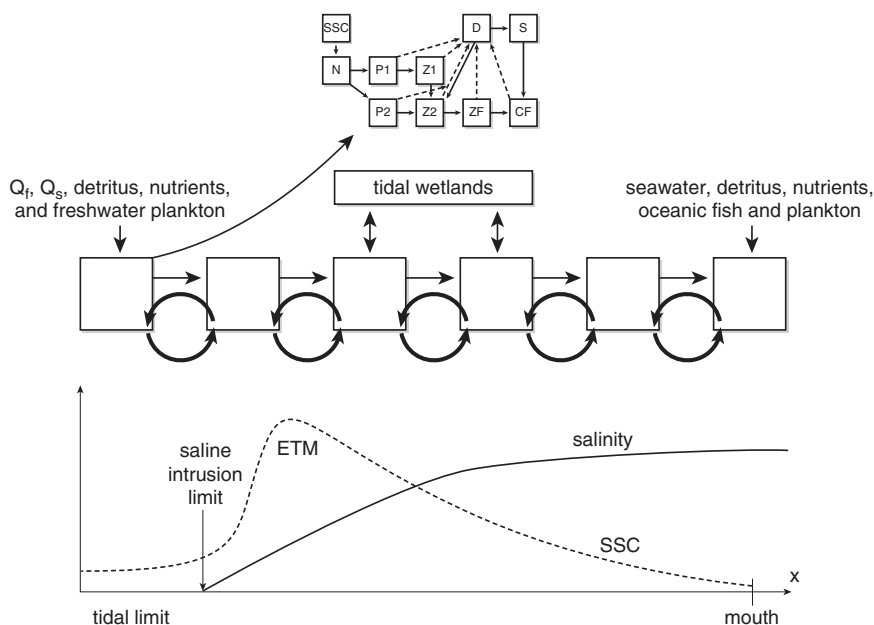

Fig. 6.8 Diagram of the structure of an ecohydrology model for mangrove estuaries (Modified from Wolanski 2007)

(Wolanski et al. 2006). This estuary is pristine but there are plans to expand the harbor and human encroachment into the estuary. The model was used to test three scenarios: (1) the impact of doubling suspended sediment concentrations through increased land clearing; (2) the impact of removing all mangroves; and (3) the impact of doubling dissolved nutrient concentrations in the upper and middle reaches of the estuary, but with no change in suspended sediment concentrations. Model outputs show that:

- In the first scenario, dissolved nutrient concentrations would quadruple in the upper half of the harbor, picoplankton abundance would increase by 50% in the middle region, total chlorophyll levels would quadruple in the middle reaches, numbers of copepod nauplii would be little affected, but adult copepods would triple in number in the middle region.
- In the second scenario, carnivorous and detritivorous fish numbers would decrease by 70% and 50%, respectively, in the upper and middle reaches of the estuary.
- In the third scenario, picoplankton numbers would increase by 50% in the upper and middle reaches, total chlorophyll concentrations would quadruple in the middle reaches, and copepod nauplii would increase by 30% in the upper and middle reaches.

The model thus suggests that ecosystem structure and function would be greatly impacted by large-scale changes in land-use.

A similar model was used to determine the fate of organic carbon in a Tanzanian mangrove ecosystem (Machiwa and Hallberg 2002). In this study, the model was composed of three submodels representing dissolved, particulate, and litter organic carbon, as well as tidal regime parameters and the size of macrofauna and microfauna communities. The model confirms empirical observations that DOC export is a major feature of this partially-impacted system, accounting for nearly 80% of organic carbon export. Forty percent of DOC is estimated to be utilized by microorganisms in order for the model to balance. The model confirms an initial premise that the extent of mangrove cover and hydrodynamic properties are strong determinants in the extent of organic carbon export from the ecosystem.

These models must be interpreted with caution, given the simplicity of the models compared with reality and the fact, in both cases, that the empirical data is inadequate for detailed calibration. Nevertheless, they are good starting points for applying ecosystems data to practical management problems.

6.7 Ecological Economics and Sustainability of Mangroves

The universal laws and concepts of ecological energetics (see Chapter 1) are analagous to some of the key principles of economics (Odum 1973; Smil 2008). The concept of ecology-economic commonality is indirectly intertwined with the fact that the energetics of ecosystems (e.g., productivity) is an important variable in

humankind's needs and activities, and in the global economy. A simple illustration of the linkage is watts = joules second^{-1}, where power (W) is simply the rate of flow of energy (J s^{-1}). This follows on from the laws of thermodynamics which also incorporate the idea that the maximum amount of work that can be derived from a reaction is related to changes in temperature, the heat content of a system, and entropy (the degree of 'disorder' in a closed system). Energy, whether identified as power or the ability to do work, is a key driver in economic production (Smil 2008). Although the field of ecological economics is concerned with energy and its usage, it inevitably focuses on the issue of sustainability.

6.7.1 Models of Resource Economics

Mangrove ecosystems provide a large number of goods and services that are utilized by humans, both commercially and on a subsistence basis (Moberg and Rönnbäck 2003). Although most resource-use models analyze the trade-off in the cost to benefit ratio of the exploitation for wood and fisheries (Barbier and Strand 1998; Grasso 1998; Janssen and Padilla 1999; Larsson and Padilla 1999; Nickerson 1999; Rönnback 1999), a few models have integrated ecological and socioeconomic limits of human resource use (Twilley et al. 1998; Ortiz and Wolff 2004).

One of the first studies to investigate the impact of mangrove loss on sustainability of fisheries was conducted for Campeche, Mexico (Barbier and Strand 1998). Using a traditional catch-effort fisheries model with equations representing changes in fishing effort in response to profit margin and changes in mangrove area, Barbier and Strand (1998) found that even a small change in mangrove area greatly impacts the shrimp harvest (Fig. 6.9). The value of the mangrove habitat in supporting the shrimp fishery is thus affected by the level of exploitation. In the long run, the economic value of the fishery will be lower if it becomes heavily depleted.

A more sophisticated modeling effort was employed by Grasso (1998) for the similar purpose of determining the trade-offs involved in maximizing wood versus fish harvesting in Brazil. Manipulating the number of workers in each industry in the models, the simulation runs reveal that the most important variable is forest growth rate, with the balance in the number of workers in each industry also dependent on the relationship between price and stock size of the resources. For instance, declining forest size results in an increase in the price of wood, but the model predicts that the number of workers will decline, shifting over to fisheries-related work. However, there is a negative feedback loop in that fishery production is directly dependent on forest area.

A similar scenario has developed in Luzon in the Philippines in which mangrove area has declined because of multiple uses that are closely interconnected (Nickerson 1999). Running a population dynamics model with a cost-benefit analysis, Nickerson (1999) found that the conflicting needs of various users (fisherman, aquaculturists, foresters, traditional users, etc.) can best we met in the long term if the mangroves are left alone (Fig. 6.10). There is little difference in the
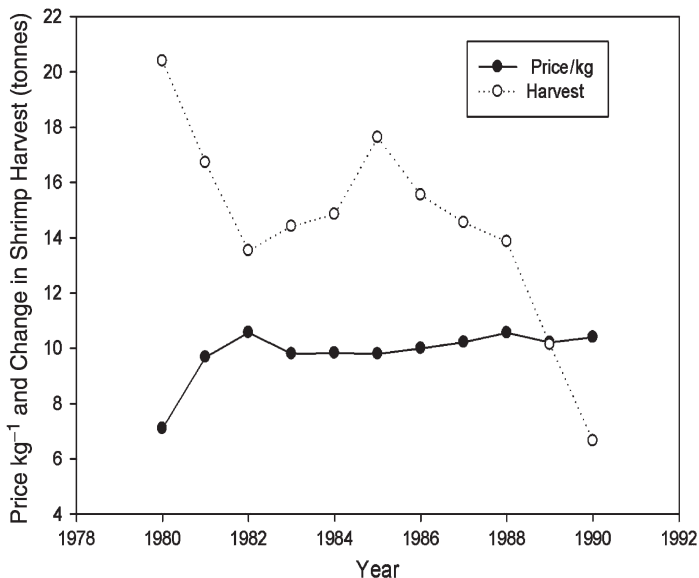
Fig. 6.9 Impact of a small decline in mangrove area (0.20%) on the price and level of harvesting of shrimp off the Campeche coast, Mexico (Data from Barbier and Strand 1998)
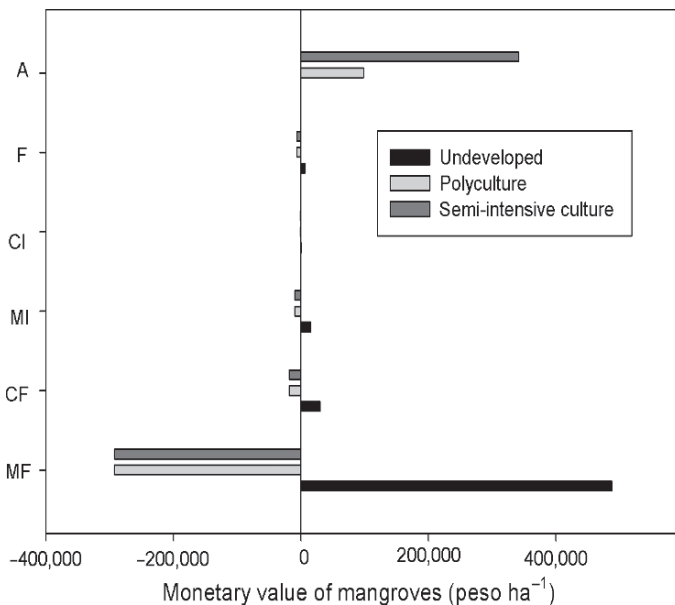

Fig. 6.10 Impact of (1) leaving mangroves undeveloped, (2) developed for polyculture of milk-fish, and (3) developed solely for shrimp aquaculture, on the monetary value of mangroves for municipal fisherman (MF), commercial fisherman (CF), municipal families using invertebrates (MI), commercial users of invertebrates (CI), foresters (F) and aquaculturists (A) in Luzon, Philippines (Data from Nickerson 1999)

value of mangroves if used either for development of milkfish polyculture or for shrimp pond aquaculture, as both scenarios greatly lessen the value of mangroves compared with leaving the mangroves undeveloped. Unfortunately, this model and another (Janssen and Padilla 1999) do not reconcile the tendency to favor short-term profit over long-term ecological and economic gain, as these areas continue to lose mangroves to human development. Mangroves continue to be undervalued economically (Rönnbäck 1999).

Models that have integrated ecological and economic constraints on unsustainable versus sustainable practices suggest more realistically that social and cultural policies must be considered (and often altered) to reconcile competing needs. For the Guayas estuary in Ecuador, Twilley et al. (1998) developed simulation models of land use to demonstrate the impact of the rate and intensity of human use on the environmental quality of the estuary. The model runs show that a 90% decline in mangrove area would result in a five fold increase in nitrogen concentrations; construction of a dam upriver, however, would result in a 60-fold increase in nutrient concentrations and a shift in intertidal and upland zones due to the decline in river discharge. A more recent model for the Caeté estuary in Brazil (Ortiz and Wolff 2004) indicates that exploitation of mangroves for wood and fisheries is currently unsustainable; a rotation harvest system is recommended for mangrove harvesting. While estimation of maximum sustainable yield of mangrove wood and other resources is urgently needed, no model can alter the fact that humans conserve what is most monetarily valuable in the short-term, especially in areas where income is limited.

6.7.2   Using Ecosystems Data to Quantify Sustainability

So how do we quantify sustainability in a meaningful way? Can the type of information and energetics approach discussed throughout this book be useful for this purpose? In order to develop strategies for sustainable management, it is important to quantify limits to sustainable harvesting, including the level of ecosystem support required to maintain production. Here we examine in more detail the managed *Rhizophora apiculata* forests in Thailand and Malaysia discussed earlier (Section 6.3.2) to show how simple models of carbon mass balance may be used as a management tool to provide preliminary estimates of sustainable wood harvesting and ecosystem support.

Strategies used to achieve sustainable timber production in tree plantations range from the application of traditional silviculture techniques to whole-forest-scale dynamic models of maximum sustainable harvesting (Fujimori 2001; Nyland 2001). Strategies applicable at the ecosystem-level have recently gained favor with silviculturalists and plantation managers in recognition of the fact that tree growth is ultimately linked to, and supported by, a host of factors operating beyond the physical limits of a particular forest. This landscape approach is based on the idea that society values forests beyond single factors such as timber production, also valuing forests for their diversity, health, and aesthetics (Rowe 1994). Strategies

based on this concept have proven successful in conserving and sustaining terrestrial forests and plantations (Raison et al. 2001).

The increase in global demand for tropical wood (Brown et al. 1997) comes at a time of declining wood yield due to environmental degradation, unsustainable harvesting practices, disease outbreaks, soil erosion, poor planning, and shortage of fresh water. It is possible that an increase in current production capacity of mangrove plantations will be needed to increase the global supply of hardwood. Mangroves are of high ecological and economic value, and their future may have to partly rely on an ecological economic approach rather than solely on conservation, especially in developing nations. A number of mangrove species are good candidates for cultivation because of their high rates of wood production. A number of plantations currently harvest mangroves, but few adhere to sustainable management practices (Saenger 2002).

A major impediment to developing strategies that can lead to sustainable timber harvesting is the lack of integrated ecological information, such as combining knowledge of factors limiting tree growth and resource use efficiency with management plans on stand rotation. Most useful techniques currently in use are based on traditional trial-and-error methods rather than on empirical scientific information.

As discussed earlier, several ecological and economic models currently exist to determine the interactive dynamics, growth, and yield of mangrove forests (Devoe and Cole 1998; Fromard et al. 1998; Berger and Hildenbrandt 2000) and to determine trade-offs between mangrove resource use and the economics of conservation (Ruitenbeek 1994; Grasso 1998; Janssen and Padilla 1999; Rönnbäck 1999; Huitric et al. 2002). Also, there have been at least two attempts to estimate the level of ecosystem support, or ecological footprint (*in sensu* Chambers et al. 2000), of mangrove ecosystems required to sustain coastal aquaculture (Robertson and Phillips 1995; Larsson and Padilla 1999). Despite this information, there are no quantifiable estimates of limits to sustainable production of mangroves or of the ecological footprint required for sustainable harvesting of mangroves. Mathematical and computer simulation models exist for estimating maximum sustainable yield (MSY) of temperate forests (Fujimori 2001; Nyland 2001), but the ecological information required to develop useful algorithms incorporating complex linkages and feedbacks for mangrove forests is insufficient.

6.7.2.1   Ecosystem-Scale Consequences of Forest Decline

While ground-truthing and GIS technology make it feasible to document habitat losses, the ability to estimate the timeframe of possible ecosystem collapse is difficult. Here we discuss how mass balance models of carbon flux in mangrove ecosystems could be used to: (1) develop estimates of sustainable wood production, (2) estimate the level of ecosystem support required to maintain yield, and (3) develop time frames for managers to avoid possible ecosystem collapse in the face of unsustainable harvesting. Data from Sawi Bay in southern Thailand and the Matang Mangrove Forest Reserve in northwestern peninsular Malaysia are used to illustrate.

The concept is simple, based on the laws of thermodynamics as applied in ecosystems ecology. If net ecosystem production is zero, the ecosystem is considered at the limit of sustainability. That is, the amount of organic matter produced or imported is equal to the amount of organic matter consumed or exported. If less than zero, the ecosystem is energetically unsustainable, at least over the long term. This is because an ecosystem that over time loses more organic matter (and energy) that it produces or gains, cannot exist for long; it will eventually disappear to be replaced by another type of ecosystem.

The term sustainability is vaguely defined in the ecological literature (Phillis and Andriantiatsaholiniana 2001), but is defined here in its simplest sense: to maintain a level of exploitation or production by restricting the quantity harvested (or extracted) to avoid long-term depletion.

A mass balance of carbon was constructed (Table 6.4) for Sawi Bay, a mangrove-fringed embayment in Chumphon province of southern Thailand. The bay is $165 \, km^2$ in area, shallow, and open to the Gulf of Thailand. The watershed and mangrove ecosystem (mostly *Rhizophora apiculata*) have seen major changes since the 1970s – increases in mussel culture, fisheries, agricultural and industrial activities, and sewage, but particularly growth of shrimp ponds (Ratanasermpong et al. 2000). The increase in both aquaculture and agriculture has resulted in severe losses of mangroves. The Royal Forestry Department now has a replanting program in place, but clearing of mangroves and adjacent forests is still taking place for agriculture, manufacturing, and commercial and housing developments. The current rate of mangrove loss is $1\% \, year^{-1}$ (Ratanasermpong et al. 2000). Possible collapse of production from the heavy losses of mangrove may occur, and government management plans specify that a time frame must be ascertained to set upper limits for continued exploitation of mangroves and the adjacent terrestrial forests.

The simple mass balance of carbon for Sawi Bay (Table 6.4) indicates that the ecosystem currently has more inputs than losses of carbon. Inputs exceed losses of carbon for a net ecosystem production of $\approx 112.6 \, mol \, C \, m^{-2} \, year^{-1}$. Most of this excess carbon is probably accumulating in biomass of replanted trees, as most mangrove forests lining the bay are ≤ 15 years old (Alongi et al. 2000c). Mangroves are the major source of energy and material flow within the bay. The mass balance also indicates that respiration from mangroves and microbes in bay waters is the greatest loss of carbon. Pelagic respiration is a relatively large loss term compared with other tropical coastal ecosystems because of the large export of metabolically active, microbial consortia from aquaculture ponds bordering the bay (Ayukai and Alongi 2000). This suggests that the bay would be sensitive to losses of mangrove forest and to increases in pond effluent.

Assuming a continuation in the decline of mangroves at $1\% \, year^{-1}$, a simulation of the changes in the mass balance equation shows that the balance of carbon flow in Sawi Bay changes from positive net ecosystem production to a carbon deficit (NEP < 0) within ≈ 27 years (Fig. 6.11). This is likely the *maximum* estimate of time until the ecosystem lapses into unsustainability. This iterative change in the mass balance neither considers increases in carbon inputs from erosion of soils, sewage, or pollutants nor the impact of growth of aquaculture ponds with corresponding
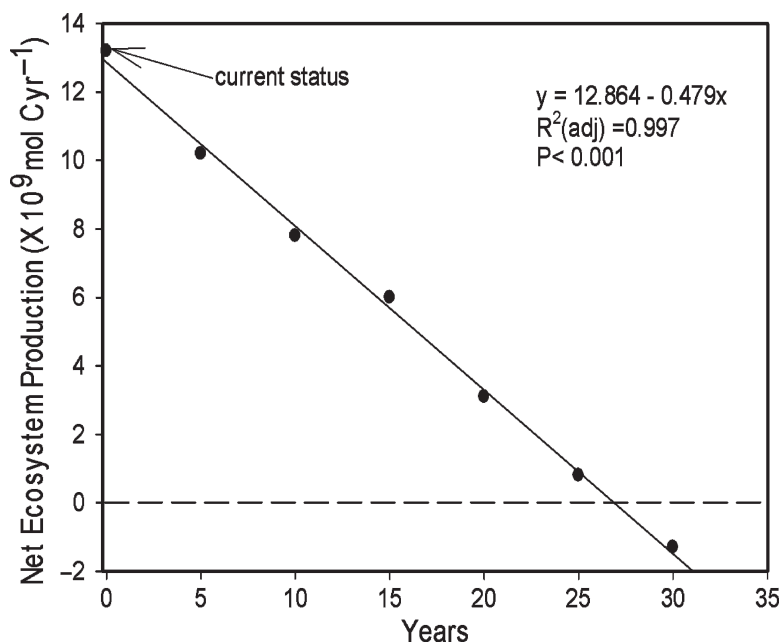
Fig. 6.11 Simulation model predicts a collapse of net ecosystem production of Sawi Bay in southern Thailand, assuming continuation of a 1% annual loss rate of mangroves. Dotted horizontal line represents the threshold of sustainability at NEP = 0 (Updated from Alongi 2005b)

increases in effluent discharge. The model also does not include complex linkages and feedback loops within the ecosystem.

The time boundary is constrained to 27 ± 10 years because the average coefficient of variation of the individual carbon measurements used in the model is ≈33%. Despite this limitation, this estimate has immediate implications for management. Felling trees without or with only limited replanting may lead to ecosystem collapse in as early as 17 years or as late as 37 years. The precautionary principle and the high certainty of both positive and negative feedback loops suggests that management plans to counter the net loss of mangroves should ensure that current rates of replanting equal or exceed current loss rates. An ecosystem that loses more carbon (and energy) than it gains can sustain itself for a limited period of time because of temporal and spatial lags and patchiness between production and consumption processes, but such an ecosystem cannot harvested indefinitely, not without restoring steady-state equilibrium (Odum 1969; Schultze 1994).

6.7.2.2 Mangrove Harvesting Limits and Ecosystem Support

The exemplar of sustainable harvesting of mangroves is the Matang Mangrove Forest Reserve in the state of Perak in peninsular Malaysia. The reserve faces the

Straits of Malacca forming a continuous 48 km belt of mangrove forest with a total area of 48,804 ha, of which 32,746 ha is classified as productive forest. The ecosystem is composed of five major estuaries, lined mostly by *Rhizophora apiculata* with an occasional understory of *Bruguiera parviflora* and *R. mucronata* along river banks (Watson 1928; Muda and Mustafa 2003). Nearly 3,200 ha of forest is conserved for research, tourism, education, a bird sanctuary, and seed stands. There is some fish cage and cockle aquaculture and fishing activity within the reserve, but only non-destructive practices are permitted.

The Matang Reserve was first gazetted in 1902 with the first working plan for sustainable harvesting and conservation completed in 1908. Under the current working plan, productive forest is managed on a sustainable basis using a 30-year rotation cycle, with two thinnings between 15–19 years and 20–24 years, with final felling at 30 years (Muda and Mustafa 2003). The thinned wood is used for poles in housing construction. The area of harvestable *R. apiculata* forest is equally proportioned between the 1- to 10-year, 11- to –20-year and 21- to 30-year-old age classes. Each year, 1,048 ha of forest is harvested in small lots for an average yield of 171 t ha^{-1} per 10 years rotation (Muda and Mustafa 2003). The annual total wood yield currently averages 17,920 t DW. The slash is left to decompose naturally or to be flushed with the tides. When felling lots, a buffer zone of 5–10 m is retained to protect against shoreline erosion. One-half of the lots are allowed to regenerate naturally, although recent problems with inadequate natural regeneration and infestation by *Acrostichum* ferns have necessitated a shift to manual planting and development of seedling banks.

Use of the wood resources in the production of charcoal is the mainstay of the local economy and management of the Matang Reserve. The forests are tendered by the Perak State Forestry Department to charcoal contactors, the number varying from 50–75, each with an average of four to five charcoal kilns. The break-even price for charcoal is about RM 400 t^{-1}; most of the produce is consumed within Perak while some is sent to market in the states of Selangor, Penang, and Kedah. Total net revenue in 2000 was RM 745,300. Net revenue fluctuates, but the total annual forest yield per hectare has remained fairly constant since first harvesting in 1906. This has been attributed to the success of maintaining and managing a balance of 20% reserve forest and 80% harvestable stands.

The mass balance (Table 6.4) shows that mangrove production and respiration dominates carbon flow within the ecosystem. Mangrove production accounts for 95% of total carbon inputs; estimated river/ocean inputs, phytoplankton production and inputs of trash fish to fish cage aquaculture are minor carbon sources. Tree respiration accounts for ≈79% of total ecosystem losses, and all respiration losses account for nearly 86% of total carbon output. Harvesting of timber and poles from thinning stages constitute relatively small losses (1% of total output), as do harvesting of natural and cultured finfish and shellfish within the reserve (5% of total output). Export of mangrove carbon is also a small loss compared with tree respiration, equating to about 5% of total carbon inputs and 24% of mangrove net primary production. Only 2% of TOC input is buried in sediments.

The reserve is producing more carbon than it is losing, with most carbon being stored in new forest growth on accreting mudbanks. Based on extensive surveys, Muda and Mustafa (2003) estimate that the reserve has gained ≈1,500 ha of new forest through accretion since its inception in 1908 (Watson 1928). This would only account for 5% of the excess carbon, but carbon may be retained as peat and as litter in some areas of the reserve. As natural and some managed tropical terrestrial forests in South America have a century-scale capacity to store carbon in wood and roots (Chambers et al. 2000), perhaps mangroves in this reserve have a similar capacity for long-term carbon storage.

Harvesting of 17.1 t DW mangrove wood year^{-1} on 1,048 ha has been sustainable for nearly a century, so assuming that the yield per unit area remains constant, we can model the change in net ecosystem production with possible incremental increases in the areal rate of wood harvesting (Fig. 6.12) using a simple computer simulation of changes to the mass balance equation. An increase in the harvest area at an incremental rate of 50% of the current rate of harvesting leads to a linear decline in net ecosystem production, assuming no complex feedback loops (Fig. 6.12). Solving the model for y = 0, the simulation predicts that 6,261 ha of
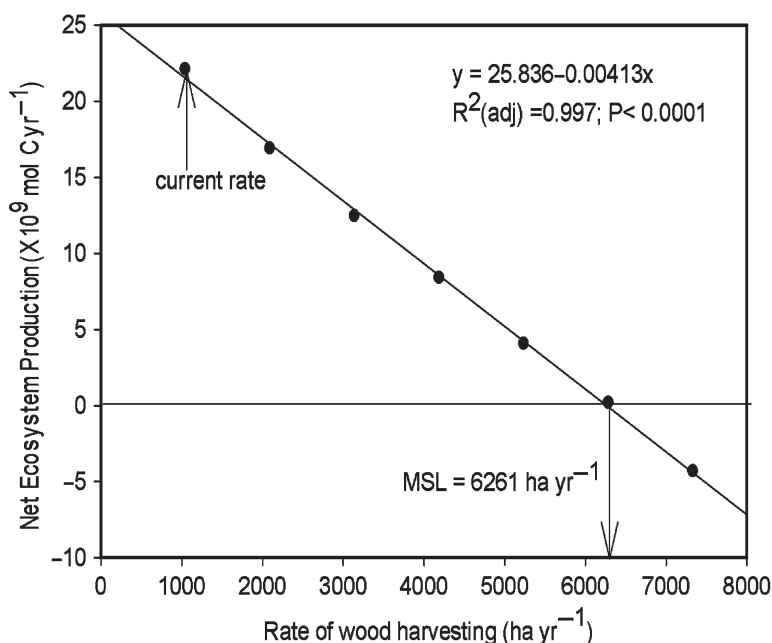

Fig. 6.12 Simulation model predicts a decline in net ecosystem production with incremental increase in rate of timber harvesting in the Matang Mangrove Forest Reserve, Malaysia. Horizontal line represents the threshold of sustainability at NEP = 0. Model run shows that a NEP of zero is attained at a rate of timber harvesting of 6,261 ha^{-1} year (Updated from Alongi 2005b)

mangrove forest year^{-1} would need to be harvested before net ecosystem production is zero and the ecosystem becomes unsustainable. This extraction rate is nearly six times the current rate of harvesting. However, the average coefficient of variation for individual flux measurements is $\approx$33%, so this translates into a predicted maximum sustainable harvest range of 4,195–8,327 ha year^{-1}. We can cautiously estimate that the current rate of harvesting can be doubled, if necessary, from 1,048 to 2,096 ha year^{-1}. These estimate does not include possible changes in within-stand yield and other changes such as an increase in fish cage aquaculture, but the model does support the fact that the current rate of harvesting is sustainable over the long term and can be increased, if desired.

Sustainable harvesting must involve some understanding of the level of ecosystem support required to service the growth and maintenance of the harvested stands. Ecosystem support is defined here as the total ecosystem area necessary to support the area under extractable use. This idea is based on the assumption that every individual organism is supported, either directly or indirectly, by various biotic and abiotic processes from the adjacent environment. This is reminiscent of the logic used to define the term 'ecological footprint' (Chambers et al. 2000). Here we assume that the area of forest under harvest is supported by the entire coastal ecosystem with the Matang Reserve comprising 8,653 ha (Muda and Mustafa 2003). Currently, the level of ecosystem support is 46.6 ha of total ecosystem area for each hectare of forest harvested (Fig. 6.13). With an incremental
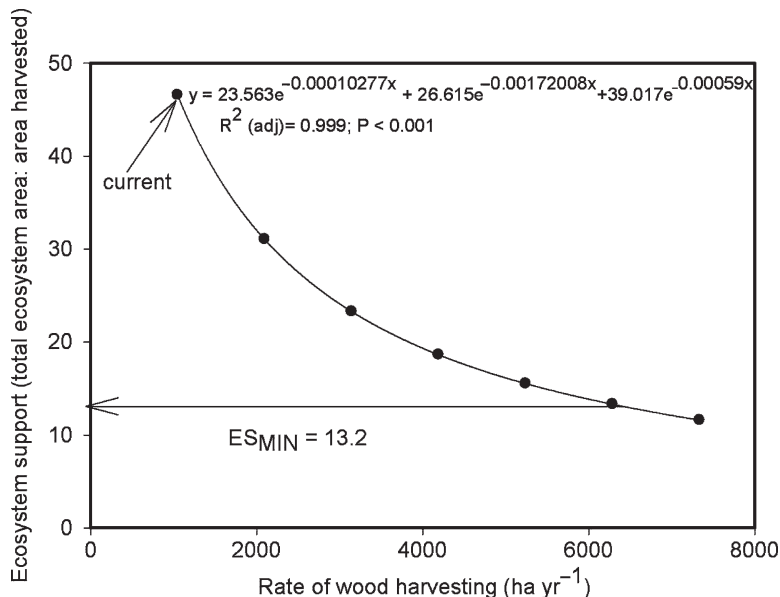

Fig. 6.13 Simulation model predicts an exponential decline in ecosystem support with incremental increase in timber harvesting within the Matang Mangrove Forest Reserve, Malaysia (Updated from Alongi 2005b)

decline in net ecosystem production as the harvested area increases, the level of ecosystem support undergoes an exponential decline when we iterate the changes in the mass balance equation in a simple computer simulation. At the predicted average maximum rate of harvesting (6,261 ha year⁻¹), when net ecosystem production is zero, the level of ecosystem support is 13.2 (Fig. 6.13). At the recommended rate of harvesting of 2,096 ha year⁻¹, the level of ecosystem support is 31 (Fig. 6.13). If we calculate changes in ecosystem support on the basis of wood yield, the index is calculated by dividing the total ecosystem area by total yield with the specific value having units of hectares per tonnes (Fig. 6.14). If the predicted maximum rate of harvesting is used, each tonne of wood harvested requires 0.46 ha of total ecosystem area for support (Fig. 6.14). At the current harvesting rate and at the recommended doubling of the harvesting rate, the level of ecosystem support required to sustain each tonne of wood harvested is 2.8 and 1.4 ha, respectively (Fig. 16.14). Similar calculations for terrestrial forests indicate a range of values of 1.0–5.7 ha t⁻¹ (Chambers et al. 2000) suggesting that the ecological dynamics of mangrove harvesting is similar to that of other forested ecosystems.

As noted earlier, few studies have attempted to estimate the level of mangrove ecosystem area required to support sustainable aquaculture (Robertson and Phillips 1995; Larsson and Padilla 1999). An estimate by Robertson and Phillips (1995) of the impact of shrimp pond effluent on mangroves indicates that if the effluent is delivered directly into forests, 2–22 ha of forest is required to totally utilize the
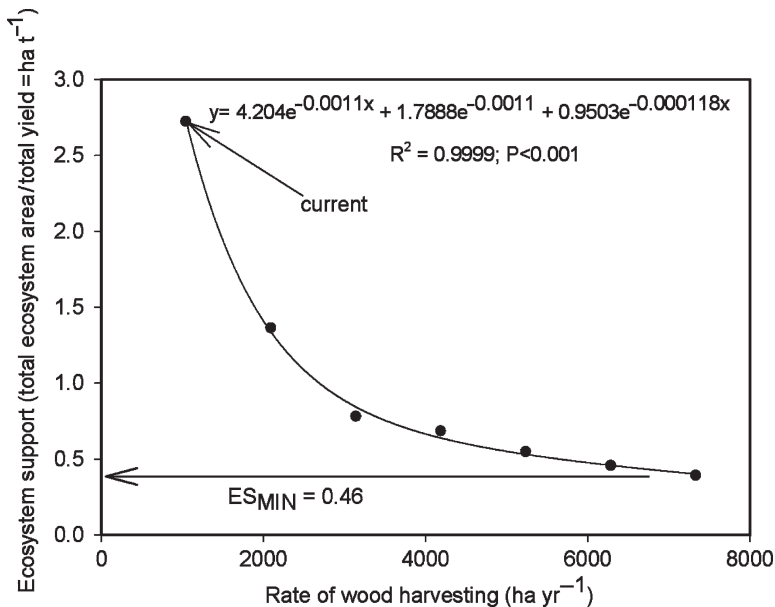

Fig. 6.14 Simulation model predicts an exponential decline in ecosystem support with an incremental increase in timber harvesting within the Matang Mangrove Forest Reserve, Malaysia (Updated from Alongi 2005b)

nitrogen and phosphorus loads from a 1 ha shrimp pond. Semi-intensive ponds require less area (2–3:1) than intensive ponds which are estimated to require an areal ratio of 7:1 to process N and an areal ratio of 22:1 to assimilate P. In a study of semi-intensive shrimp farming in Colombia, Larsson et al. (1994) estimates that 35–190 ha of mangrove ecosystem is needed to support each ha of pond, as more than 80% of the primary production required to feed shrimp stock is derived from adjacent ecosystems. Aquaculture within mangrove ecosystems ranks as one of the most resource-intensive systems and can be characterized as unsustainable.

The mass balance estimates of the exploitation of mangrove forests in Thailand and Malaysia are not absolute, but are intended to show that comparatively simple models based on empirical data can quantify estimates of uppers limits of sustainable use of resources. Practical management needs relatively simple and practical approaches for approximating upper limits to sustainable production and ecosystem support. Mass balance models cannot be used in isolation from other information in order to set management plans; they do have limitations. For instance, the iterative adjustments to the mass balance do not take into account linkages and feedbacks among ecosystem components. It is almost certain that a change in the rate of harvesting would affect detrital outputs (e.g., more slash on the forest floor) that would in turn affect the rate of carbon loss via microbial respiration, and so forth. More complex models would have to refine these estimates to account for such interactions.

Regardless of the accuracy of the mass balance calculations, the first example from southern Thailand underscores the consequences of unregulated or poorly managed mangrove cultivation and felling. The Malaysian example illustrates best-practice methods in sustainable extraction of mangrove timber and offers a valuable lesson for estimating limits to sustainability of other *Rhizophora apiculata* plantations. The level of ecosystem support for *Rhizophora apiculata* in the Malaysian scenario is 2.76 ha t^{-1}. This estimate is well within the range of 1–5 ha t^{-1} estimated for terrestrial plantations (Chambers et al. 2000). This similarity suggests that methods and practices used to manage the harvesting of terrestrial trees of a similar age span and with similar growth rates can be applied to *Rhizophora apiculata* plantations. As illustrated here, many functions of mangrove forest ecosystems appear to be more similar to their terrestrial forest counterparts than their aquatic neighbors.